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Journal of Experimental Marine Biology and Ecology 317 (2005) 13–24

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Effects of nutrient enhancement on the fecundity of a coral reef macroalga

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Received 14 May 2002; received in revised form 18 August 2004; accepted 3 November 2004

Abstract

On coral reefs, there is concern that increased nutrient supply (e.g. due to eutrophication) causes increased algal growth and hence increased algal abundance, in turn causing colonisation and invasions of coral populations, resulting in reef degradation, or a coral–algal phase shift. For example, species of *Sargassum*, a highly seasonal, large, brown seaweed, are suggested to be colonising corals on inshore coral reefs of the Great Barrier Reef, as a result of anthropogenic increases in terrestrial runoff of sediments and nutrients. However, implicit in this argument is the assumption that nutrient-related increases in growth will lead to increased fecundity (and/or propagule success), since without such changes, increased abundance can only occur by vegetative means. Whilst plausible, there is no experimental evidence for this assumption in coral reef algae.

We here present an initial study in which experimental increases in nutrient supply apparently did not lead to increased fecundity of *Sargassum siliquosum*; rather, density and biomass of receptacles were reduced in nutrient-enhanced algae. There was little effect of nutrient treatments on the proportional allocation of biomass to reproductive and vegetative structures: nutrient enhancement led to similar decreases in biomass of reproductive and vegetative tissue. Tissue nutrient levels indicated effective enhancement of nitrogen supply, although phosphorus levels were not different across nutrient treatments.

The reduced fecundity with increased nutrients may reflect either a genuine inhibition by higher nutrient levels, as found in previous studies, or accelerated maturation, causing increased tissue losses due to more advanced seasonal senescence. Either way, this exploratory experiment provides initial evidence that nutrient effects on tropical coral reef macroalgae may be complex, and does not support the assumption that increased nutrient supply will result in a numeric increase in populations of *Sargassum* spp. Our results should not be taken as an unequivocal demonstration that nutrients inhibit fecundity overall, but illustrate the need to distinguish between effects on different life-history processes (e.g. growth and reproduction). For increased

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doi:10.1016/j.jembe.2004.11.013

growth of pre-existing individuals to contribute to algal invasions and phase shifts, that growth must result in either increased fecundity, or increased propagule success.

Keywords: Algae; Coral reef phase shifts; Fecundity; Nutrient effects; Reproduction; *Sargassum*

1. Introduction

Reproduction and recruitment are critical processes in the dynamics of ecological populations and communities, and fecundity, or reproductive output, is a key aspect of reproduction and supply-side ecology, one that may exert considerable control over the abundance of species at a site (e.g. for marine algae; Santelices, 1990; Lobban and Harrison, 1997). In many marine ecosystems, and on many coral reefs in particular, there is concern that increased inputs of nutrients, or eutrophication, may lead to increased algal abundance, resulting in so-called "phase shifts" in which, in the case of coral reefs, abundant corals are replaced by abundant algae (Morand and Briand, 1996; Lapointe, 1997; Raffaelli et al., 1998; see discussion in McCook, 1999; Hauxwell et al., 2000). For example, on the Great Barrier Reef (GBR), Australia, it has been suggested that increased inputs of terrestrial nutrients have led or could lead to increases in abundance and distribution of the large, canopy-forming macroalgae, *Sargassum* (Bell and Elmetri, 1995; Furnas and Brodie, 1996; Schaffelke and Klumpp, 1998a).

However, it is important that these processes (phase shifts and increases in algal abundance) be considered not only in the context of ecological interactions such as herbivory (Hughes, 1994; McCook, 1999; Jompa and McCook, 2002), but also in the context of the processes of reproduction, such as fecundity, dispersal, and recruitment (Davis et al., 2000). An increase in abundance of algae may involve either or both of two processes: (i) growth of existing algae, resulting in more algal tissue per unit area; or (ii) increases in area occupied by the algae. Increased algal biomass within an area involves increased height or density, whether of algae with distinct individuals (e.g. *Sargassum*) or those with turfing growth forms (e.g. algal turfs), and assumes herbivory is insufficient to prevent accumulation of algal growth. An increase in area occupied by algae may involve either (a) vegetative expansion of existing algal thalli onto new substrate, a process with limited scope for large-scale changes; or (b) colonisation by propagules from the plankton, thus involving a numeric increase. In the latter case, increased colonisation may involve one or more of increased fecundity, increased settlement, or post-settlement survival. In taxa such as *Sargassum*, with distinct individuals and minimal vegetative reattachment, increases in area occupied must involve numeric increases.

Most previous work demonstrating nutrient enhancement of growth in coral reef algae has overlooked the detailed aspects of these population level processes. This work often implicitly assumes that demonstrated increases in algal growth will necessarily lead to increases in area, presumably either through increased reproductive output or through increased viability of propagules (Lapointe, 1997; Schaffelke and Klumpp, 1998a). This assumption, specifically postulated by Ang (1985), is entirely reasonable in principle (Weiner, 1988; De Wreede and Klinger, 1988), but has apparently not been experimentally tested, at least for tropical species. There is experimental evidence, primarily from temperate marine algae, demonstrating important roles for factors such as temperature, photoperiod, and light, in regulating fecundity (Lüning and Dieck, 1989; Santelices, 1990; Lobban and Harrison, 1997). However, the relationship between nutrients and algal reproductive development and fecundity is much less clear, and the available evidence suggests it may vary, depending on species, life histories, nutrient levels, and supply, etc. (Hoffmann et al., 1984; Reed et al., 1996; Coelho et al., 2000). Furthermore it has not been demonstrated that algal growth and reproduction are limited by the same resources (De Wreede and Klinger, 1988).

Given that algal invasions and phase shifts are unlikely to occur without numeric increases in algal populations, and the importance of such invasions

during coral reef degradation, there is a need for experimental tests of the relationship between nutrients and algal fecundity on coral reefs (Santelices, 1990; Lobban and Harrison, 1997). We present here an initial experimental exploration, examining whether nutrient enhancement affects the fecundity or reproductive output of an abundant coral reef seaweed (*Sargassum siliquosum* J. Agardh) in a controlled environment. Although by no means a comprehensive test, the results suggest that enhanced nutrient supply may not lead to increased fecundity.

2. Methods

2.1. General approach and experimental design

To explore the effects of nutrient enhancement on the fecundity (reproductive biomass allocation) of *S. siliquosum*, we applied experimental nutrient pulses to the algae in outdoor tanks and tested the effects on the number and biomass of reproductive structures (receptacles). The experimental design involved three levels of nutrients: ambient (control), medium, and high, each with five replicates (or tanks), with three fertile adult thalli in each tank. We chose to do the experiment during the reproductive season, to ensure thalli were fertile, and because nutrient pulses occur in the field during this period. Inshore reefs in this area are frequently exposed to intense nutrient pulses from flood plumes during the austral summer (concentrations in the flood plumes reach 12.8 μM NH_4 and 2.5 μM PO_4, Devlin et al., 2001). However, it is important to recognise that there may be a critical period for nutrient enhancement and that a comprehensive study would involve nutrient treatments at several different stages of the seasonal growth cycle, a major undertaking beyond the scope of the present study.

2.2. Study species, collection, and sample preparation

Species of *Sargassum* have been implicated in degradation of coral reefs worldwide (Bouchon et al., 1992; Hughes, 1994; Bell and Elmetri, 1995), and both temperate and tropical species appear to have considerable invasive potential (Paula and Eston, 1987; Critchley et al., 1990; Stiger and Payri, 1999a,b). We selected *S. siliquosum* as one of the most abundant algae in the central section of the GBR (McCook et al., 1997; personal observation); together with other species of *Sargassum*, it forms dense canopies on the reef flats and slopes of inshore reefs of the GBR. Most *Sargassum* populations in this area are highly seasonal, producing abundant reproductive structures (receptacles) during the austral summer. These receptacles are shed during autumn, dispersing propagules. After the reproductive season, *S. siliquosum* thalli die but the holdfast and stems remain, for at least several years (Morrissey, 1980; Price, 1989; Martin-Smith, 1993; Vuki and Price, 1994; McCook, 1996; Schaffelke and Klumpp, 1997a; Umar et al., 1998; personal observation).

Adult *S. siliquosum* plants were collected in March 2000 from the fringing reef (1–4 m depth) on Goold Island (18°10′85″ S; 146°10′05″ E), in the inshore, central GBR. This reef is very close to sources of terrestrial nutrients and sediments; further description of the study area can be found in McCook (1996, 2001). At the time of specimen collection, nutrient concentrations at the site (at 2 m depth) ranged between 0.02 and 0.04 μM for NH_4, and between 0.05 and 0.07 for μM PO_4, although, concentrations vary considerably within short periods of time (McCook, 2001; Devlin et al., 2001).

Fertile female plants of 30–40 cm height, with healthy growing apical tips and few epiphytes, were collected, with the attached substrate (carbonate rubble or rocks), and transplanted to the outdoor aquarium at the Australian Institute of Marine Science (AIMS). Initial length and wet weight (blotted dry) of each thallus were measured prior to nutrient manipulations. Algae were kept in running seawater (except during nutrient pulse treatments), in 70-l plastic "nally" bins throughout both transplantation (1 day) and experimental periods (30 days); at the AIMS aquarium, bins were immersed in larger tanks with flowing seawater, to regulate temperature, and aerated to enhance mixing, especially during nutrient additions. Experimental thalli were cleaned regularly of epiphytes with a cloth.

2.3. Nutrient enhancement protocols

Nutrient manipulations involved a nutrient pulse protocol comprising addition of nutrients for a 24-h

period every 7–11 days for 30 days, using reagent-grade ammonium chloride and sodium dihydrogen-phosphate (Schaffelke, 1999). We used nutrient pulses rather than continuous supply mainly because they more realistically simulate events such as flood plumes or resuspension events, which represent major nutrient inputs to reefs in this region (Furnas and Brodie, 1996; Russ and McCook, 1999; Schaffelke, 1999; Devlin et al., 2001), not only because this allows direct comparison with previous studies in this area and with this genus (Schaffelke and Klumpp, 1998b), but also because it is logistically difficult to sustain both viable aquarium conditions and reliable concentrations of nutrients in large tanks for this duration. The experimental duration (30 days) was based on the duration of receptacle formation and maturation, shown to be less than a month for several species of *Sargassum* (Yoshida et al., 2001). We applied three nutrient concentration treatments: (1) Ambient, untreated controls, using seawater from the AIMS mariculture system (average concentrations ranged between 0.02 and 0.19 μM of NH_4, and between 0.01 and 0.37 μM of PO_4); (2) Medium, with ≈5 μM of NH_4 and 0.5 μM PO_4; and (3) High, with ≈10 μM NH_4 and 1 μM PO_4. The concentrations, ratios, and duration of these nutrient pulses are within the ranges recorded on inshore reefs in this area, and the duration and frequency of pulses based on previous physiological studies (Schaffelke and Klumpp, 1998b; Schaffelke, 1999; Devlin et al., 2001). Concentrations were confirmed using three replicate samples of filtered water (0.45μm Sartorium Minisart), frozen immediately after collection and later analysed in an autoanalyzer at AIMS (Ryle et al., 1981). Seawater (ambient and enriched) was replaced every 4–6 h during the 24-h pulse.

To measure the effectiveness of the nutrient manipulations, we analysed tissue nutrient concentrations in the vegetative and reproductive tissues of *S. siliquosum* at the end of the experiment. Tissue nutrients (C, N, P) were determined from 5 replicates per nutrient treatment. Algal tissue was dried at 60 °C for 48 h, ground, and the concentrations of C and N determined with a Perkin Elmer CHN Analyzer. P was determined using ICP analysis (Ryle et al., 1981).

2.4. Response variables and data analyses

At the end of the experiment, each thallus was measured (length), cleaned of epiphytes, rinsed in freshwater, and the receptacles removed, counted, and both vegetative and reproductive (i.e. receptacles) tissues weighed wet and dry (60 °C for 48 h). The number and dry biomass of receptacles are used as indices of fecundity, as biomass allocated to reproduction is considered a good descriptor of the relative reproductive output (Bäck et al., 1991). Proportional reproductive allocation or proportional reproductive investment was estimated as the percentage of receptacular dry biomass/total vegetative dry biomass (Mathieson and Guo, 1992). The differences between initial and final length and wet biomass were used as measures of growth during the course of the experiment. The allocation of

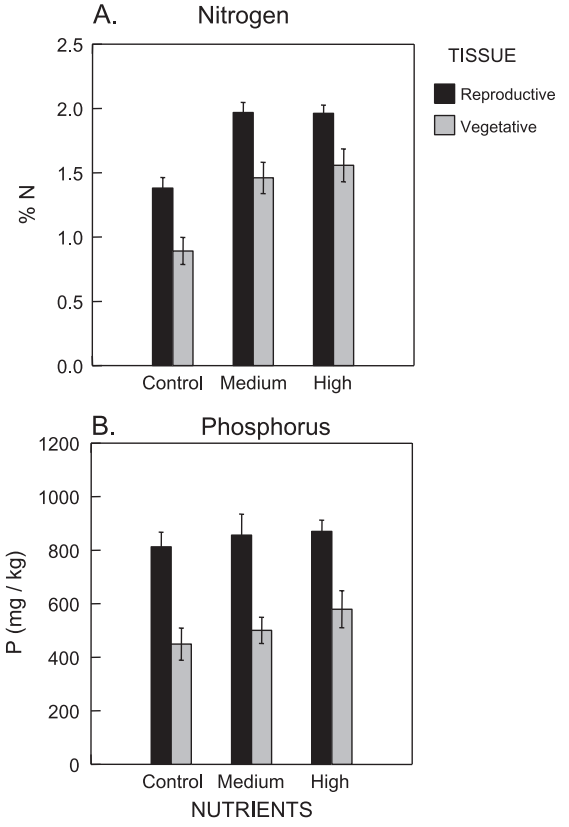

Fig. 1. Mean tissue nutrient concentrations of nitrogen (A) and phosphorus (B) of reproductive and vegetative tissue of *Sargassum siliquosum* across nutrient treatments (±1 S.E., *N*=5).

nutrients to reproductive and vegetative tissues was compared using the ratios of tissue concentrations in the two tissues for each thallus.

Data analyses included one-way ANOVA and SNK tests to test for effects of nutrient enrichment on the number of receptacles, dry biomass of receptacles, dry biomass of vegetative tissue, proportional reproductive biomass allocation, and on growth. The ANOVA model included three nutrient levels as fixed factors and five replicates, these being the average of the three thalli in each nally bin. Effects on growth involved four to five replicates per nutrient treatment (loss of labels in some tanks prevented before-after comparisons, resulting in fewer replicates). Paired *t*-tests were used to compare the initial and final length and wet biomass within each nutrient treatment. The effects of nutrient enhancement on tissue nutrient concentrations within vegetative and reproductive tissue types, and the proportional allocation of nutrients to the two tissues, were analysed using one-way ANOVAs, with 5 replicates per treatment; post hoc comparisons used Tukey's test. Tissue nutrients were also compared between the two tissues using paired t-tests. All data were checked for normality graphically, using stem and leaf plots and probability plots; and for homogeneity of variances with Cochran's test, on which bases data were not transformed.

3. Results

3.1. Test of treatments: tissue nutrient concentrations

Nutrient treatments resulted in clear enhancement of algal tissue nitrogen, but the effects on tissue phosphorus were less clear. Both tissue concentrations (per gram algal tissue) of nitrogen and N:C ratios of both reproductive and vegetative tissues were significantly higher in the nutrient addition treatments than in unenriched controls (Fig. 1a; Table 1). There were no significant differences in tissue nitrogen between medium and high nutrient treatments for both reproductive and vegetative tissues, suggesting saturation at the medium nutrient treatment. Phosphorus levels (per gram algal tissue) in both reproductive and vegetative tissues were ranked according to the nutrient treatments, but the differences were smaller and not significant, and P:C ratios showed little differences across nutrient treatments (Fig. 1b; Table 1). Tissue nitrogen and phosphorus concentrations were significantly higher in the reproductive tissue than in vegetative tissue at all levels of nutrient treatment (Fig. 1; for N: control: t=6.990, df=4, P=0.002; medium: t=3.582, df=4, P=0.023; high: t=2.907, df=4, P=0.044; for P: control: t=6.293, df=4, P=0.003; medium: t=3.415, df=4, P=0.027; high:

Table 1
ANOVAs of effects of nutrient enhancement and type of tissue (reproductive or vegetative) on the tissue N and P concentrations and on the N:C and P:C ratios of *Sargassum siliquosum*

Source of variation	Reproductive tissue					Vegetative tissue			
	df	MS	*F*	*P*	Tukey's test	MS	*F*	*P*	Tukey's test
N (%)									
Nutrients	2	0.570	25.87	<0.0001	C<M≈H	0.647	11.92	0.0014	C<M≈H
Error	12	0.022				0.054			
N:C ratio									
Nutrients	2	0.0004	16.29	0.0004	C<M≈H	0.0004	11.31	0.0017	C<M≈H
Error	12	0.00003				<0.0001			
P (mg/kg)									
Nutrients	2	4421.4	0.316	0.736	C≈M≈H	21521.4	1.560	0.250	C≈M≈H
Error	12	14000.7				13795.6			
P:C ratio									
Nutrients	2	<0.0001	0.096	0.909	C≈M≈H	<0.0001	0.889	0.436	C≈M≈H
Error	12	<0.0001				<0.0001			

C=unenriched control, M=medium nutrient concentration, H=high nutrient concentrations.

t=4.427, df=4, P=0.011). The proportional allocation of nutrients to the two tissues was not significantly different among nutrient treatments (one way ANOVA, P=0.19 for N and P=0.55 for P), although there was a consistent trend to reduced allocation to reproductive tissues in thalli from the enhanced nutrient treatments.

3.2. Fecundity: receptacle number and reproductive biomass

Nutrient enrichment reduced the apparent fecundity of *S. siliquosum*. The number and biomass of reproductive structures (receptacles) were significantly lower in treatments where nutrients were added (Fig. 2a, b; Table 2). Receptacle counts from unenriched control thalli were almost 60% higher than those for thalli from the medium and high nutrient enrichment treatments (Fig. 2a) and reproductive biomass of the control treatment was about 50% higher than that in the medium and high nutrient enrichment treatments (Fig. 2b). There were no significant differences in either measure between medium and high nutrient treatments.

The dry biomass of vegetative tissue in the control treatment was also significantly higher than in the medium and high treatments (Fig. 2c; Table 2). There was no significant difference in vegeta-

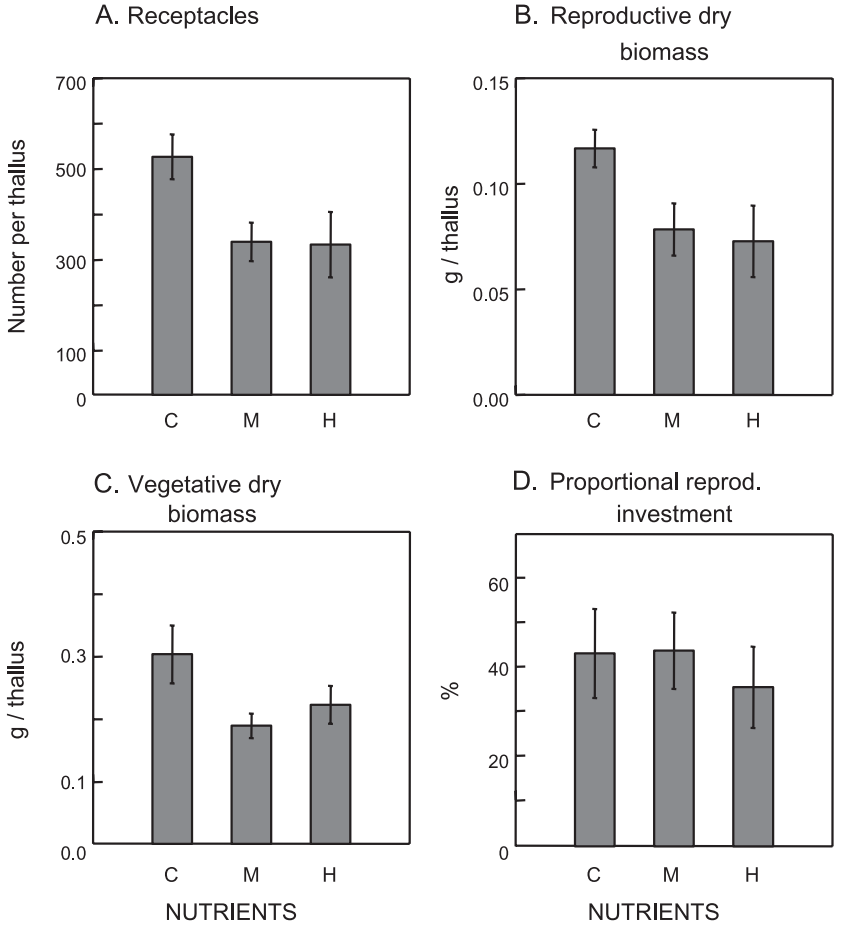

Fig. 2. Mean number of receptacles (A), reproductive dry biomass (B), vegetative dry biomass (C), and proportional reproductive investment (D) per thallus of *Sargassum siliquosum* across nutrient treatments (C=unenriched control, M=medium nutrient concentration, H=high nutrient concentration; ±1 S.E., N=5).

tive biomass of the medium and high nutrient treatments.

3.3. Proportional reproductive biomass allocation (proportional reproductive investment)

Despite the apparent differences in reproductive output per *S. siliquosum* plant, we did not detect a significant effect of nutrient enrichment on the proportional allocation of biomass to reproduction (reproductive dry biomass/vegetative dry biomass; Fig. 2d; Table 2). Although proportional reproductive investment in the high nutrient treatment was slightly lower than the other two treatments, this difference is unlikely to represent a real effect (type II error) as it was highly non-significant and is not consistent with the patterns seen in the receptacle counts and biomass measures.

Table 2
ANOVAs of effects of nutrient enhancement on the number of receptacles, reproductive and vegetative dry biomass, proportional reproductive investment, and on the difference between initial and final lengths and total wet biomass of *Sargassum siliquosum*

Source of variation	*df*	MS	*F*	*P*	SNK test
Receptacle number					
Nutrients	2	60530.5	5.01	0.026	C>M=H
Error	12	12075.6			
Reproductive dry biomass					
Nutrients	2	0.00286	4.30	0.039	C>M=H
Error	12	0.00066			
Vegetative dry biomass					
Nutrients	2	0.01724	3.89	0.049	C>M≈H
Error	12	0.00443			
Proportional reproductive investment					
Nutrients	2	0.01043	0.32	0.734	N.S.
Error	12	0.03280			
Difference in length					
Nutrients	2	0.331	0.02	0.985	N.S.
Error	10	21.825			
Difference in total wet biomass					
Nutrients	2	19.489	3.94	0.055	H>C=M
Error	10	4.946			

C=unenriched control, M=medium, H=high nutrient concentrations. NS=not significant.

3.4. Growth: initial vs. final length and total wet biomass

Thallus length did not show significant changes between initial and final measurements within any level of nutrients (control: $t=-0.342$, $df=4$, $P=0.75$; medium: $t=-1.122$, $df=3$, $P=0.344$; high: $t=-0.521$, $df=3$, $P=0.639$; Fig. 3a), suggesting that growth in terms of thallus length was negligible over the course of the experiment. Further, there were no significant differences between treatments in those changes in length (Table 2).

Although the length of the algae did not vary, thalli lost significant amounts of tissue during the experiment, through the shedding of secondary branches, leaves, vesicles, and receptacles. This was reflected in the differences in wet biomass, which was significantly reduced by the end of the experiment, in both the unenriched control ($t=3.27$, $df=4$, $P=0.031$) and at the high nutrient treatments ($t=6.26$, $df=3$; fewer replicates due to loss of labels, $P=0.008$; Fig. 3b); although the difference was not significant at the medium nutrient treatment ($t=1.76$, $df=3$, $P=0.177$). The extent of the differences between the initial and final biomass varied almost significantly across nutrient treatments: thalli of the high nutrient treatments lost proportionally more biomass than thalli from the control and medium treatments, in part because initial wet weights were higher (but not significantly so, $P=0.210$) in the high nutrient treatment (Fig. 3b; Table 2). Analysis of covariance (ANCOVA, details not shown) using the initial wet weights as covariate did not indicate a significant effect of initial wet weight on the response variables (receptacle number, reproductive biomass, or investment), and gave similar results for treatment effects as the one-way ANOVA.

4. Discussion

The results of this experiment strongly suggest that nutrient enhancement should not be assumed to lead to increased fecundity and recruitment in benthic macroalgae, as widely assumed. In these experiments, nutrient enrichment apparently reduced the reproductive output of mature *S. siliquosum*, in contrast to, and potentially counter-acting, effects on growth rates

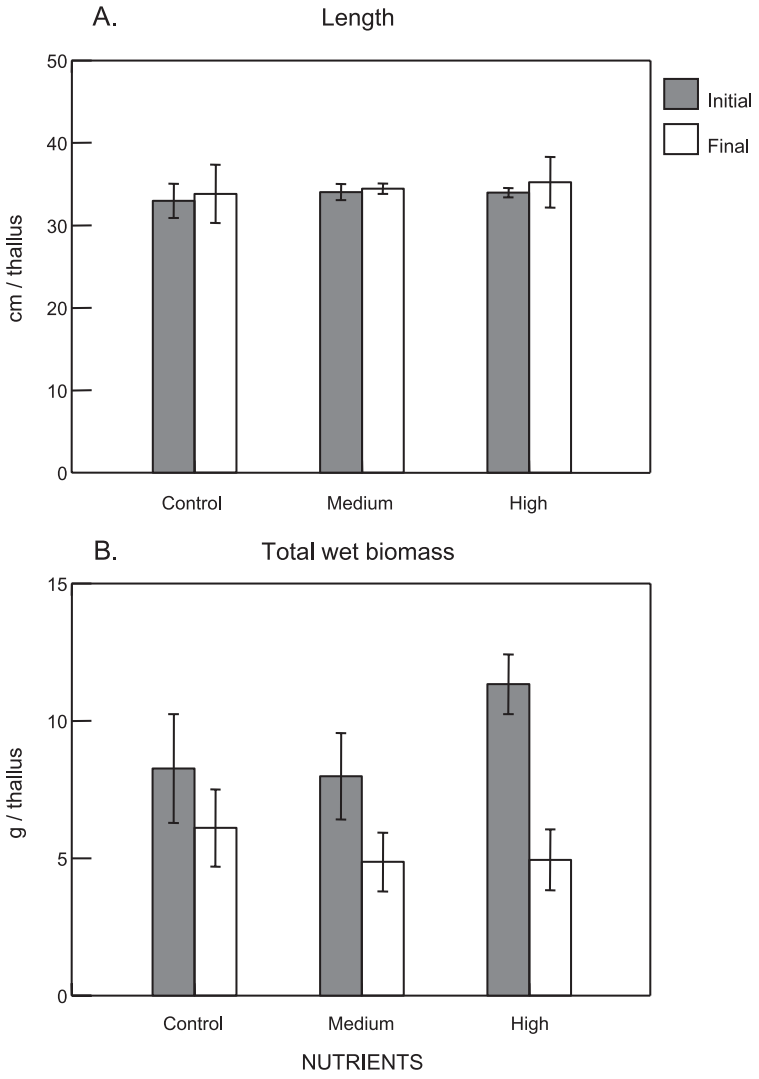

Fig. 3. Mean length (A) and total wet biomass per thallus (B) of *Sargassum siliquosum* at the beginning (initial) and end of the experiment (final) across nutrient treatments (±1 S.E., $N=4–5$).

(Larned, 1998; Schaffelke and Klumpp, 1998a). The number and biomass of reproductive structures (receptacles) were lower in treatments where nutrients were added, and the proportional allocation of biomass to reproductive tissues, whilst not significantly reduced, was clearly not enhanced by nutrient additions. The vegetative biomass was also similarly reduced by nutrient enrichment, suggesting that these nutrient additions were generally detrimental to fertile adult plants (Fig. 2). The patterns in length and biomass data are consistent with seasonal patterns in the field, with cessation of thallus growth and initial shedding of distal tissues. Importantly, the length of the thalli did not decrease, indicating that thallus senescence was not far progressed.

Although these results contrast with general assumptions about nutrients and fecundity, those assumptions, whilst reasonable, appear to stem from little direct evidence. Ang (1985), also working with tropical *S. siliquosum*, correlated growth with phosphate concentrations, and postulated a link to fecundity. Hoffmann et al. (1984) found that development of

different reproductive stages of a temperate kelp had variable nutrient requirements, and fertilisation had a relatively narrow optimal range of concentrations; this would not suggest a simple, monotonic relationship between concentrations and fecundity. Also working with temperate kelps, Reed et al. (1996) found contrasting correlations between reproductive allocation and seawater temperature, in two different kelps, and inferred relationships with nutrient availability (based on temperature–nutrient correlations). They suggested that nutrient resources might enhance fecundity in species that reproduce continuously but not in species that that are strictly seasonal. Our results for *S. siliquosum*, which is strongly seasonal in reproduction, would be consistent with this suggestion. As previously pointed out (De Wreede and Klinger, 1988), algal growth and reproduction may be limited by different resources. The effects of nutrient increases on algal fecundity seem likely to be complex and difficult to generalise.

It is important to recognise that there are limitations to the context of our study, which therefore should not be taken as unequivocal demonstration that nutrients reduced the overall fecundity of this species, but rather as demonstration that nutrient increases may not result in increased fecundity, and that further experimental evidence is required. For example, it is possible that the apparent reduction in reproductive output and biomass in nutrient enhancement treatments reflects either (i) a genuine inhibition, or even toxicity; (ii) accelerated maturation, with consequent increased tissue losses due to more advanced senescence.

The concentrations of nutrients used in this experiment have been widely used in both adults (Schaffelke and Klumpp, 1998b) and early life stages (Schaffelke and Klumpp, 1997b; Diaz-Pulido and McCook, 2003) of other local species of *Sargassum* and in other fleshy macroalgae (Jompa and McCook, 2002), generally with neutral or positive effects, but there is evidence for inhibition of *Sargassum* growth at high nutrient levels (McCook et al., 1997; Schaffelke and Klumpp, 1998a). High nutrient levels have also been shown to inhibit early life-history stages of other large brown seaweeds, but the mechanisms behind that inhibition remain unclear (Ogawa, 1984; Hoffmann et al., 1984; Doblin and Clayton, 1995; Kevekordes, 2001; Burridge and Bidwell, 2002; Bergström et al., 2003). If reproductive processes like fertilisation have optimal nutrient concentrations (Hoffmann et al., 1984), then reductions in reproductive output at higher nutrient levels are not unlikely, but it is also possible that the mechanisms involve a toxic effect of higher levels of nutrients. Elevated nutrient concentrations, particularly of ammonium, may inhibit algal photosynthesis by altering the electron transport chain, and may affect enzyme and membrane functions due to the inability of the cell to buffer protons released from ammonium assimilation (Peckol and Rivers, 1995; Kevekordes, 2001; Bergström et al., 2003).

However, given the patterns of biomass losses among treatments, we cannot discount the second interpretation, that our nutrient enhancement treatments resulted in earlier onset of propagule release, so that low receptacle counts may be an artifact of more advanced tissue senescence. Nonetheless, this interpretation is not supported by the observation that proportional tissue losses were no different between control and medium nutrient treatments, and even if timing of onset were earlier, this would still not provide evidence of increased reproductive output.

The timing of nutrient enhancement in relation to developmental processes may be important (Hoffmann et al., 1984), so it is also possible that nutrient enhancement at other periods (e.g. during pre-reproductive stages) may have different effects to those in our study. Complete appreciation of nutrient effects may not only require experiments at different times, but may need to integrate the outcome of contrasting effects at different stages, may be dependent on the timing or seasonality of actual nutrient events in the field, and is very likely to vary between species (Santelices, 1990).

Similarly, although previous work (Bäck et al., 1991) indicates that receptacle density or biomass provides a good proxy for overall reproductive output, it is important to recognise the potential for nutrient effects on numbers of conceptacles per receptacle, on oogonia per conceptacle, or even on the viability or growth rates of planktonic or settled propagules. Clearly, full consideration of all possible effects, and of timing, was beyond the scope of the present study, and detailed interpretation of the processes underlying our results will require further experimental evidence on a range of species.

Thus, we interpret our results as providing initial evidence for the potential complexity of nutrient effects on the potential for algal invasions, and, importantly, as illustrating the need to distinguish between effects on growth, and effects on fecundity or recruitment processes, and consequent invasion potential. Furthermore, even if fecundity or propagule viability was enhanced, this would not necessarily result in population increases, since hydrodynamics of dispersal, and pre- and post-settlement mortality may overwhelm fecundity effects. In the context of coral reef phase shifts, there is strong evidence that algal abundance, distributions, and invasions are less strongly affected by growth rates (and nutrient supply) than by reductions in herbivory, by overfishing or diseases (Hughes, 1994; McCook, 1999; Hughes et al., 1999; Jompa and McCook, 2002), or by coral disturbances that create new free substrate for algal settlement and colonization (Aronson and Precht, 1997; Williams et al., 2001; Diaz-Pulido and McCook, 2002). In the specific case of putative invasions by *Sargassum* of inshore reefs on the GBR, available evidence does not indicate that increased nutrient inputs alone can be assumed to cause increased invasions of *Sargassum*. Not only are *Sargassum* distributions strongly influenced by herbivory (McCook, 1996, 1997), but the strong seasonal cycle of growth, reproduction, and senescence may mean any nutrient related gain in growth is negated by intrinsic upper limits to biomass per thallus, perhaps due to intraspecific competition or physical constraints, and completely negated during seasonal senescence.

In summary, our results did not provide evidence that increases in nutrients will result in increased fecundity of this highly seasonal, coral reef seaweed, since the number and biomass of reproductive structures decreased with nutrient additions during the reproductive period. The complexity of the processes involved means that these results can only be taken as initial indications, and should not be taken as proof that nutrients inhibit fecundity overall. However, they do illustrate the need to distinguish between effects on different life-history processes. Whatever the effects on growth and biomass of pre-existing algae, growth of individuals does not necessarily result in growth of populations. For nutrients to enhance algal invasions requires both (i) that the nutrient enhancement increases either fecundity or propagule viability, and (ii) that fecundity or viability affect final recruitment (Davis et al., 2000). The present results do not support the first requirement. In the context of coral reef degradation, this provides further demonstration that the documented and serious consequences of eutrophication are unlikely to simply involve increases in algal growth and consequent replacement of coral populations (Ginsburg, 1994; Wilkinson, 2000; McCook et al., 2001), but are likely to involve complex interactions between processes.

Acknowledgements

This study was supported by the Australian Institute of Marine Science, CRC Reef, School of Tropical Biology, James Cook University, and the Instituto Colombiano para el Desarrollo de la Ciencia y Tecnología—COLCIENCIAS. Special thanks to C.P. Arango, J. Bohórquez, D. Moreno, F. Olivier, and J. Jompa for invaluable help in the field and laboratory, and to C.D. Amsler, M.J. Anderson, P. Ang, S. Connolly, G. Kendrick, B. Santelices, B. Schaffelke, and two anonymous reviewers for ideas and discussion. **[AU]**

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